
A SURVEY OF THE REPRODUCTIVE BIOLOGY OF THE MYRTOIDEAE (MYRTACEAE)¹

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ABSTRACT

The Myrtoideae usually present small, epigynous, 4–5-merous, polystemonous flowers that last one day. Bee-pollination in which pollen is the sole reward is the dominant pollination system. Nectar has been best documented in *Syzygium* but probably also occurs in other bee-pollinated genera. The most common bee visitors are Apidae: Meliponinae and Bombinae. Bird- and mammal-pollination occur in Old World *Syzygium* with nectar as the primary reward. Bird-pollination with petals as the reward occurs in New World *Acca* and *Myrrhinium*. General floral morphology is very uniform, while inflorescence types and flowering strategies are very diverse. Stigmas are dry and ovules are anatropous, hemicampylotropous or anacampylotropous and have an outer 2–6-layered integument and an inner 2-layered integument or a single integument. The ovary usually contains more ovules than will form seeds. Flowering strategies vary from mass-flowering types, in which the flowering episode typically takes only a few days, to steady-state types of up to 90 days duration. Flowering at dry/wet season transition is common in seasonal climates, and fire-induced flowering is found occasionally. Outbreeding is probably widespread, although both self-compatible and self-incompatible species exist. The self-incompatible species have self pollen tubes penetrating the micropyles, so preferential outcrossing may be maintained by a late-acting mechanism. Cryptic dioecy, in which female flowers have “mimic” sterile anthers occurs in several genera. Apomixis occurs in *Syzygium* and this has been reported to be linked to the polyembryony found in this genus. Myrtoid fruits are fleshy berries or drupes, dispersed by birds, bats, and other small mammals. Fruit size, color, texture, and number of seeds are all very variable. Seed coats may be absent to bony, but have a smooth surface. The endosperm is mainly digested by the developing embryo. Early embryology is relatively uniform but final embryo morphology varies widely across the genera. Germination times vary from 10 days to over 2 years and seed viability periods from 15 days to 1 year.

The reproductive biology of the Australian Myrtaceae has recently been the subject of a thorough review by Beardsell et al. (1993). The alliances traditionally assigned to the subfamily Leptospermoideae are the major focus of their account, reflecting not only the predominance of these groups in the Australian flora but also the widely acknowledged dearth of information on the reproductive biology of the Myrtoideae in general (e.g., van Wyk & Lowrey, 1988; Proença & Gibbs, 1994).

The present survey was compiled to complement that of Beardsell et al. (1993) by bringing together the scattered and often fragmentary data on the Myrtoideae. We use the term Myrtoideae in the traditional

sense to embrace virtually all the fleshy fruited Myrtaceae. Thus we include Johnson and Briggs's (1984) monophyletic Myrtoideae sensu stricto, and their *Acmena* alliance (including *Syzygium*), although phylogenetic analysis has suggested that this latter group is more closely related to the leptospermoid *Eucalyptus* alliance than to the Myrtoideae s. str. (Johnson & Briggs, 1984). Conversely, we use the term Leptospermoideae in its broadest sense to include all Myrtaceae with capsular fruit. Where names have been changed to fit modern taxonomic concepts, the name that appeared in the original publication is cited in parentheses, e.g., *Syzygium paniculatum* (as *Eugenia paniculata*).

¹ This survey is based largely on a portion of the doctoral thesis of the first author, funded by the Royal Botanic Gardens Kew, UK, with substantial contributions from the doctoral thesis of the second author, funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil. Both theses were prepared under the supervision of Peter Gibbs of the University of St. Andrews, Scotland, and the authors gratefully acknowledge his guidance and encouragement in the field and in the laboratory, as well as his critical reading of the present manuscript. Pranom Chantaranonthai, Martin Cheek, John Wyndham Dawson, Keith Ferguson, Madeline Harley, Ray Harley, Bruce Holst, Jim Jarvie, Leslie Landrum, John Parnell, Alan Paton, Susanne Renner, Paula Rudall, Peter G. Wilson, Elizabeth Woodgyer, and Daniela Zappi also read and made improvements to various versions of this paper, while J. W. Dawson, Keyt Fischer, Maria A. S. Alves, and Anthony Raw provided unpublished data; we thank them all for their patience and interest. The first author owes a great debt of thanks to the library staff at the Royal Botanic Gardens, Kew, for their unfailing cooperation and support and, in particular, to Ann McNeil who facilitated an online search of the BIOSIS bibliographical database.

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The pantropical Myrtoideae as a whole has not received any synthetic taxonomic treatment since Niedenzu's (1893) synoptic account. There is no Old World equivalent to McVaugh's (1968) invaluable review of the American Myrtoideae. As a subfamily the Myrtoideae are rather less morphologically diverse than the Leptospermoideae. Approximately 60 genera are recognized for the estimated 2375 species of Myrtoideae, while the Leptospermoideae with less than half the number of species (1300) includes some 72 genera (species numbers from Schmid, 1980; generic estimates reflect the present authors' view of current taxonomic opinions). While this discrepancy may be interpreted as an artifact of our ignorance of the former group, most myrtologists would agree that the perceived homogeneity is real and has contributed to, rather than resulted from, the comparative taxonomic neglect which this subfamily has indisputably suffered. McVaugh (1968) described the species of American Myrtaceae as "distressingly alike in aspect and in most individual characters, making identification and classification of both genera and species a correspondingly difficult and tedious matter."

This homogeneity is portrayed in more concrete terms in Schmid's (1980) table of the "distinguishing organographic characters of the subfamilies of the Myrtaceae," the majority of which are based on reproductive organs. For each character a statement of the prevailing state within each subfamily is followed by a summary of the exceptions. Schmid expressed the estimated percentage of exceptions using precise and clearly defined qualifying terms: "very rarely" (signified < 2% of species), "rarely" (2–4%), "very occasionally" (5–10%), "occasionally" (5–30%) and "often" (31–60%). Hence a reasonably accurate impression of the variability of particular characters within the subfamilies can be gained. The qualifier "very rarely" is applied to the majority of the exceptions listed for the Myrtoideae. In the Leptospermoideae, however, exceptions are more or less evenly distributed across the range from "rarely" to "often" with "very rarely" being applied in only two instances. Thus the Myrtoideae emerges as a much more homogeneous group than the Leptospermoideae.

INFLORESCENCE STRUCTURE

Inflorescences may be apical, subapical, axillary, supra-axillary, ramiflorous or cauliflorous in position. The authoritative analysis of inflorescence structure in the Myrtaceae by Briggs and Johnson (1979) documented an equally impressive range of

structural form within the Myrtoideae. They range from many-flowered panicles and thyrsoids through dichasia, botryoids, metabotryoids, triads, and metaxytriads to monads and metaxymonads. In their brief description of adaptive syndromes, these authors drew attention to correlations between habitat, niche, and inflorescence arrangement. In particular, large panicles or aggregations of smaller inflorescences are reported by them as typical of forest and woodland species of Myrtaceae (myrtoid examples include species of *Myrcia* and its allies, *Blepharocalyx* (as *Temu*), *Pimenta*, *Xanthomyrtus*, species of *Syzygium* and its allies). However, in the undergrowth or understory of non-sclerophyllous communities, they noted that flowers are often in monads and/or triads that are not massed (myrtoid examples include *Myrceugenia*, *Psidium* spp., *Ugni*, *Myrteola*, *Myrtus* sensu stricto, *Rhodamnia*, *Lophomyrtus*, *Neomyrtus*, *Campomanesia*, *Luma*, and *Eugenia* spp.) (Briggs & Johnson, 1979). Ramiflorous or cauliflorous inflorescences have been linked to bat pollination (Crome & Irvine, 1986), and to bat or marsupial dispersal (see Fruit Characteristics and Dispersal Agents).

FLOWER STRUCTURE

Flowers of the Myrtoideae are hermaphrodite (or very rarely unisexual), epigynous (or very rarely semi-epigynous), with (3–)4–5(–8) sepals and (0–)4–5(–6, 12) petals per flower. The perianth parts are free in bud or occasionally form a calyptra or operculum or rupture irregularly at anthesis. In several genera the individual calyx lobes or the hypanthial remnants are deciduous after anthesis. Petals are white, cream, pale pink, or (rarely) deep pink or red. Stamens are usually numerous but, when few, the androecium may be diplostemonous, haplostemonous, or obhaplostemonous (i.e., a univerticillate androecium with only antipetalous stamens; Schmid, 1980). Stamens are generally free and attached directly to the hypanthium, but fascicled stamens occur in a few species of *Syzygium* sometimes segregated as *Pareugenia* (Schmid, 1972a). Most Myrtoideae have a secretory cavity at the apex of the anther connective but this feature is lacking in a handful of species in various genera (Schmid, 1972a). Carpels, when present, are 2 or occasionally 3–18 per flower, and the number of ovules per ovary is usually many, occasionally few, and very rarely one. General flower structure varies little among species as compared to other larger families, but flower size may vary by an order of magnitude.

ANTHER DEVELOPMENT AND MICROSPOROGENESIS

The anther is tetrasporangiate and dehiscence is by longitudinal slits. In *Gomidesia* the thecal margins are often strongly inrolled, so that the interior of the sacs and the pollen are only exposed over a small area at the apex (and often another small area at the base) of the anther. *Gomidesia* anthers have often been termed poricidal; however, they are more accurately described as longitudinally dehiscent and functionally poricidal. Terminally dehiscent anthers have also been reported in *Acmena*. The anther sacs, which are almost globose and somewhat divaricate, open by a terminal slit and are one of the diagnostic features of this genus (Merrill & Perry, 1938). Pollen grains of all Myrtoideae (and all Myrtaceae) studied to date are two-celled at anthesis (Schmid, 1984[1985]).

POLLEN GRAINS

Patel et al. (1984) reviewed the palynological literature on the Myrtaceae. Pike's (1956) survey of 300 species in 71 genera remains the most comprehensive work on the subject to date. Although her study focused on the Leptospermoideae of the southwest Pacific area she also investigated representatives of the Myrtoideae, including some South American genera, and was forced to conclude "There appears to be no particular feature that separates the pollen of the Myrtoideae from that of the Leptospermoideae" (Pike, 1956: 46).

Barth and Barbosa (1972) confirmed the stenopalynous nature of the Myrtoideae on the basis of their survey of 140 species in 19 genera. They described myrtoid pollen as follows (translated from the Portuguese original with modern preferred terms (Punt et al., 1994) inserted [in brackets] after outmoded terms): "grains small to medium, oblate to peroblate, tricolporate with lalongate ora [endoapertures], goniotreme [angulaperturate] with triangular amb [polar view], surface of apocolpia and mesocolpia granular, smoother near the apertures. On average sexine is twice as thick as nexine 2 [endexine], which is constant in thickness. The sexine is tectate, the bacula [columellae] being responsible for the granular surface of the grains; undulations on the surface originate from the tectum. Nexine 1 [foot layer] is limited in occurrence; in general it is absent or reduced to fragments in grains with a thicker exine" (Barth & Barbosa, 1972: 468–469).

All these features common to the Myrtoideae are also characteristic of the Myrtaceae as a whole. Both Pike (1956) and Patel et al. (1984) recognized three pollen types in the Myrtaceae: (1) longicol-

pate, (2) syn- or parasyncolpate, and (3) brevi- or brevissimicolpate grains. All members of the Myrtoideae studied were reported to have grains of one or the other of the first two types, grains of type (3) being confined to certain members of the *Chamelaucium* group. However, Barth and Barbosa (1972) reported grains of all three types in the Myrtoideae and listed some 25 instances where both longicolpate and syncolpate grains were found in the same species, usually in the same collection, as most species in this study were represented by a single specimen. Similar variation was reported in about one third of the 18 species studied by Lieu and Melhem (1973), while most of the remaining species sampled had consistently longicolpate grains.

Pollen is released as free monads except in *Myrtus communis* L. and *Psidium cattleianum* Sabine (as *Psidium littorale* Raddi) where there is a mixture of free monads and tetrahedral tetrads (Patel et al., 1984). Dimorphic pollen occurs in association with cryptic dioecy in *Decaspermum parviflorum* (Lam.) A. J. Scott (Kevan & Lack, 1985) and in the South African species of *Eugenia* (van Wyk & Lowrey, 1988; van Wyk & Dedekind, 1985). Male flowers produce normal pollen grains and female (apparently hermaphrodite) flowers produce morphologically abnormal unviable pollen grains.

STIGMA AND STYLE STRUCTURE

Beardsell et al. (1993) described stigmas in the Myrtaceae as unspecialized and generally of the "wet" type, citing the Heslop-Harrison and Shivanna (1977) review of the receptive surfaces of the angiosperm stigma. In fact, Heslop-Harrison and Shivanna (1977) recorded dry stigmas with unicellular papillae in five of the seven genera of Myrtaceae studied, including all three of the myrtoid genera in the survey (*Acca* (as *Feijoa*), *Eugenia*, and *Syzygium*). Dry stigmas were also reported for the six genera studied by Proença and Gibbs (1994) (*Blepharocalyx*, *Campomanesia*, *Eugenia*, *Myrcia*, *Psidium*, and *Siphoneugenia*) and in *Gomidesia* (Nic Lughadha, pers. obs.) and thus appear to represent the norm in the Myrtoideae.

Stigmas are undivided or very rarely divided. Bifid or occasionally trifid stigmas are reported in the African species *Eugenia ancorifera* Amshoff (Amshoff, 1974), *E. aschersoniana* F. Hoffm., and *E. mossambicensis* Engl. (Amshoff, 1958). Schmid (1980) drew attention to the style and stigma of *Campomanesia guazumifolia* (Cambess.) O. Berg, which has been variously described as "shortly bifid," "broadly capitate," and "peltate." Most Myrtoideae have punctiform or capitate stigmas. Proen-

Table 1. Correlations between stigma diameter, ovule number, and pollen tubes.*

Species (number of flowers per obs.)	Stigma diameter (mm)	Max. number of ovules	Max. number of pollen tubes
<i>Blepharocalyx salicifolius</i> (8 fls)	0.1	12	±35
<i>Campomanesia pubescens</i> (6 fls)	0.74	78	±20
<i>Campomanesia velutina</i> (4 fls)	0.57	29	±50
<i>Eugenia dysenterica</i> (3 fls)	0.1	8	±15
<i>Myrcia linearifolia</i> (3 fls)	0.1	4	17
<i>Myrcia rhodosepala</i> (3 fls)	0.1	6	10
<i>Psidium firmum</i> (3 fls)	0.65	298	±120
<i>Siphoneugena densiflora</i> (3 fls)	0.1	13	±15

* Adapted from Proença (1991).

ça (1991) reported both types in a study of eight species and went on to demonstrate a positive correlation between stigma diameter and ovule number (Table 1). This was explained in terms of the need for the stigma of a multi-ovulate flower to support more germinating pollen grains. The dioecious *Pimenta dioica* (L.) Merr. and the putatively dioecious *P. guatemalensis* (Lundell) Lundell are exceptions, having very low ovule numbers (1–4 per ovary) and large peltate stigmas. Proença (1991) argued that the females of these dioecious species no longer need to minimize stigma size in order to avoid deposition of self-pollen and consequent inbreeding depression (in the case of a self-compatible species) or occupation of all the ovules by self-pollen tubes and subsequent abortion of the pistil (in the case of a self-incompatible species) and suggested that expanded stigmas optimize pollen collection from the pollinator's body, the only pollen source for a totally female plant. *Carpolepis elegans* (Montrouzier) J. Wyndham Dawson, the only known dioecious Leptospermoideae, also has a large peltate stigma in contrast to the punctiform stigmas of its hermaphrodite congeners (Dawson, 1992).

OVARY STRUCTURE

The ovary comprises 2(3–18) fused carpels. The locules are generally multi-ovular, but the number of ovules is often reduced and very rarely each locule may contain only a single ovule. Axile placentation is the norm but parietal, basal, and apical placentation have also been reported (Schmid, 1980). Where placentation is axile a compitum (a passageway connecting the loculi) is often present. Carr and Carr (1961) commented that, because of their relationship to the styler canal(s), such compita may increase the chance of fertilization where

pollination is limited. Pollen tubes were observed growing through compita in *Siphoneugena densiflora* O. Berg and *Myrcia linearifolia* Cambess. (Proença, 1991).

OVULE STRUCTURE AND MEGAGAMETOPHYTE DEVELOPMENT

The extremely uniform embryology of the Myrtoideae was noted by Mauritzon (1939). Recent reviews by Tobe and Raven (1983) and Beardsell et al. (1993) have shown that subsequent studies have added few genera to the list studied by Mauritzon and have done little to dispel the original impression of uniformity within the Myrtoideae.

Ovules of the Myrtoideae (as of the Myrtaceae as a whole) are generally described as anatropous, crassinucellate, and bitegmic. Mauritzon (1939) commented "I hardly exaggerate when I say that there is no other great family in the plant kingdom in which the ovules of the species so regularly have two invariably two-layered integuments." He then proceeded to describe the fusion of these two-layered integuments to form a single integument of four cell layers in material which he referred to as *Eugenia paniculata* Banks ex Gaertn. (almost certainly *Syzygium paniculatum* Gaertn.). Unitegmic ovules have also been reported in *Syzygium cumini* (L.) Skeels (Narayanaswami & Roy, 1960a; Roy & Sahai, 1962 (as *S. caryophyllifolium* (Lam.) DC.)), *Syzygium fruticosum* DC. (Roy, 1961 (as *Eugenia fruticosa* L.)), *Syzygium jambos* (L.) Alston (van der Pijl, 1934 (as *Eugenia jambos* L.)), *Syzygium malaccense* (L.) Merr. & L. M. Perry (van der Pijl, 1934; Roy, 1960 (as *Eugenia malaccensis* L.)), and *S. myrtifolium* (Roxb.) DC. (Roy, 1962 (as *Eugenia myrtifolia* Roxb.)). Van Wyk and Botha (1984) commented that those *Eugenia* species for which only a single integument has been described in the literature can probably all be referred to *Syzygium*. Tobe and Raven (1983) discussed the possible origin and significance of unitegmy in *Syzygium*. Few would dispute their conclusion that it represents a derived feature within the basically bitegmic Myrtales. However, their proposition that unitegmy "probably will be found in other genera when the family is better known embryologically" (Tobe & Raven, 1983: 86) has yet to be substantiated.

Mauritzon's generalization about myrtaceous integuments seems to hold true insofar as it concerns the inner integument: where this is distinct from the outer integument it is nearly always two cell layers thick (locally three cell layers thick in some South African *Eugenia* species (van Wyk & Botha, 1984)). However, the outer integument in the Myr-

toideae has proved more variable than Mauritzon's survey led him to suspect. Petit (1908, quoted in Mattos, 1989) reported 4 cell layers in the outer integument of *Luma apiculata* (DC.) Burret (as *Myrceugenia apiculata* (DC.) Nied.) and commented that the outer integument may comprise even more layers in some species of *Eugenia* judging by the considerable thickness of the integument of *Myrcianthes pungens* (O. Berg) D. Legrand and *Eugenia uniflora* L. (cited as *Eugenia pungens* O. Berg, and *Stenocalyx michelii* O. Berg, respectively). Van Wyk and Botha (1984) described an outer integument four to six layers thick over the greater part of its free length in their detailed study of South African *Eugenia*.

This latter group of *Eugenia* also seems to represent an exception to the generalization that ovules of the Myrtoideae (and the Myrtaceae) are anatropous. Van Wyk and Botha (1984) reported hemicampylotropous ovules (occasionally tending to be ana-campylotropous) and suggested that campylotropous ovules have frequently been taken as anatropous during cursory investigations.

In all Myrtoideae studied to date the micropyle is formed from both integuments. As in other Myrtaceae, embryo-sac formation in the Myrtoideae follows the *Polygonum*-type pattern and the antipodal cells are ephemeral (Tobe & Raven, 1983).

FLOWERING

FLOWERING SEASONALITY

Data on the time of initiation of flowering in the Myrtoideae have been compiled and discussed by Proença (1991) and Proença and Gibbs (1994). A tendency to flower at the dry/rainy season transition was distinguished, a pattern exhibited by 6 of the 8 species (in 6 different genera) studied by them in the Distrito Federal, central Brazil, and 7 out of 10 species of Myrtoideae investigated in other South American forest communities by other researchers (Frankie et al., 1983; Ferreira & Merona, 1987; Morellato et al., 1989). This pattern was clearly demonstrated in a floristic study of the Myrtaceae of the Serra do Cipó, Minas Gerais, Brazil, in which Kawasaki (1984, 1989) reported that the majority of the 50 species (in 11 genera) recorded for the area were found flowering in September and October (spring), after the first rains in the region. Two of these species had a second flowering period in February and March (late summer/early autumn), and a further five species flowered only during this latter period. In Costa Rican dry forest *Eugenia salamensis* Donn. Sm. was the only mass-flowering species (out of 21 mass flowerers studied) to bloom

at the beginning of the wet season (Frankie et al., 1983). The other species (not Myrtaceae) bloomed during the long dry season. Ruiz and Arroyo (1978) reported flowering by *Eugenia* sp. at the beginning of the wet season in a Venezuelan deciduous forest. Proença and Gibbs (1994) proposed that flowering may be cued by abrupt increases in humidity, which are much more frequent at the dry/rainy season transition than during the remainder of the year. Landrum (1986) commented that most species of *Campomanesia* flower in the spring, usually in October in southeastern Brazil and adjacent regions. In contrast, most species of the temperate and subtropical South American genus *Myrceugenia* flower during the summer and autumn with a relatively small number of species flowering during late winter and spring (Landrum, 1981). Chilean Myrtaceae flower during the dry spring and summer (Landrum, 1988).

Southern African Myrtoideae exhibit a strong conformity to spring dry/wet season flowering, with 12 of the 15 species of *Eugenia* studied by van Wyk and Lowrey (1988) conforming to this pattern. The remainder flower in early summer (two species) or in winter (one species). Spring flowering is also reported as the norm in southern Australian Myrtaceae (Beardsell et al., 1993; O'Brien & Calder, 1993), though this generalization may be more applicable to the capsular dry-fruited Myrtaceae than to the Myrtoideae, as no specific examples from this latter group are cited. In fact, two detailed studies of Australian species of the genus *Syzygium* illustrate the variation in the time of flowering within this large genus. In Kuranda, northern Queensland, the rainforest tree *Syzygium tierneyanum* (F. Muell.) T. G. Hartley & L. M. Perry flowered in January (Hopper, 1980) while *S. cormiflorum* (F. Muell.) B. Hyland, another northern Queensland rainforest tree, had an extended flowering period ranging from at least late July to mid-November (Crome & Irvine, 1986). In Indonesia, however, at least one species of *Syzygium* does appear to demonstrate the dry/wet season transition spring flowering pattern discussed by Proença and Gibbs (1994): in Sulawesi trees of *Syzygium lineatum* (DC.) Merr. & L. M. Perry (as *Syzygium syzygioides* (Miq.) Merr. & L. M. Perry and subsequently corrected) flowered in February and March (spring) toward the end of what appeared to be "a fairly dry season"—precise information on climate was not available (Lack & Kevan, 1984). In the same area *Decaspermum parviflorum* (Lam.) A. J. Scott flowered in January and February, apparently toward the end of a short dry period (Kevan & Lack, 1985).

FLOWERING DURATION, PATTERN, AND SYNCHRONY

Meager though the data on flowering seasonality may appear, information on flowering strategies is scarcer still. Proença and Gibbs (1994) described four flowering strategies observed in the Myrtaceae of the Distrito Federal, central Brazil. Of these, three corresponded to types described by Gentry (1974) viz., "big bang," "cornucopia," and "steady state" flowering, and the fourth, for which they coined the term "pulsed bang," is a modification of the big bang strategy from which it differs in its discontinuity: flowering days may be followed by intervals of several days when no flowers are open. Such pulsed bang flowering was reported in *Myrcia rhodosepala* Kiaersk. and in *Blepharocalyx salicifolius* (Kunth) O. Berg in central Brazil. Kevan and Lack (1985) described a similar pattern in *Decaspermum parviflorum* in Sulawesi. In this species flowering occurred regularly once in every two or three days with all plants in synchrony over the peak blooming time from late January to mid-February. The total flowering period of ca. 4 weeks was, however, considerably shorter than the ca. 8-week periods estimated for the central Brazilian pulsed-bang species.

Also in Sulawesi, *Syzygium lineatum* had a total flowering period of approximately the same duration as the nearby *Decaspermum parviflorum* (ca. 4–5 weeks) but, as far as we could tell, appeared to exhibit a typical cornucopia pattern (Lack & Kevan, 1984). *Siphoneugena densiflora* in central Brazil also exhibited the cornucopia strategy with many flowers being produced per plant over a period of a month or so and a population flowering period estimated at 8 weeks.

The distinction between the cornucopia strategy and the steady state strategy in which relatively few flowers are produced each day over a long period of time may be somewhat arbitrary in some instances. The central Brazilian shrubs *Psidium firmum* Berg and *Campomanesia pubescens* (DC.) Berg, with flowering periods of ca. 12 weeks, were considered steady state (Proença & Gibbs, 1994). The Amazonian tree *Psidium acutangulum* DC. had an even longer flowering period. Flowering was reported all year round with relatively few flowers being produced from January to March (Falcão et al., 1992). Similar patterns were reported for other Amazonian fruit crops studied by these authors, including *Eugenia stipitata* McVaugh and *Myrciaria dubia* (Kunth) McVaugh (Falcão et al., 1988, 1989). The term steady state seems inappropriate for these latter species, as monthly totals for flower production exhibit spectacular peaks and dips. A better

example of steady state flowering is provided by the northern Queensland species *Syzygium cormiflorum*, which has a rather long flowering period (> 14 weeks) and apparently relatively few flowers open per day. Crome and Irvine (1986) commented that "flowers are not numerous" and that their experimental program was limited by "insufficient flowers."

Syzygium tierneyanum, also from northern Queensland, appears to represent the opposite extreme of flowering strategy, viz., the classic big bang. The species is described as bursting into flower and reaching its peak over a 12-day period. Hopper (1980) counted 334 flowers per cubic meter of lower canopy and estimated that a 20-m plant could carry ca. 300,000 flowers at its seasonal peak. The central Brazilian species *Eugenia dysenterica* DC. and *Campomanesia velutina* (Cambess.) O. Berg also exemplify the big bang strategy, albeit on a smaller scale (Proença & Gibbs, 1994), as does *Eugenia salamensis*, a dry forest species in Costa Rica (Frankie et al., 1983).

Two Costa Rican dry forest shrubs, *Eugenia oerstediana* O. Berg and *Psidium guineense* Sw., exhibit a multiple bang strategy, flowering several times a year in synchronized flowering episodes lasting less than two weeks (Suarez & Esquivel, 1987).

LONGEVITY OF INDIVIDUAL FLOWERS

One-day flowers are the norm in the Myrtoideae. Species in which individual flowers last one day or less were reported from *Blepharocalyx*, *Campomanesia*, *Decaspermum*, *Eugenia*, *Myrcia*, *Myrciaria*, *Psidium*, *Siphoneugena*, and *Syzygium* (Hopper, 1980; Kevan & Lack, 1985; Peters & Vasquez, 1986/87; Proença & Gibbs, 1994). Stratton (1989) reported a mean floral longevity of 1.27 days, and a range of 1.1–1.5 days for three myrtaceous species in Costa Rican cloud forest. In this study of 110 species, in 35 families, taxonomic constraints at family level were the most important determinant of floral longevity, explaining 73% of the variance. Singh and Sehgal (1968) reported that the stigma of *Psidium guajava* L. is receptive for 2 or 3 days. Primack (1985), however, included the Myrtaceae in a list of families with long-lived flowers, which typically last 4–19 days. This generalization was very likely based on examples from the Leptospermoideae in which long-lived flowers appear to be common, e.g., flowers of *Leptospermum scoparium* J. R. Forst. & G. Forst. may last up to 3 weeks (Primack, 1980). Such longevity is rare in the Myrtoideae and where it occurs appears to be positively

associated with large flower size, e.g., *Syzygium cormiflorum* has flowers of ca. 4 cm in diameter, which do not brown until one week after anthesis (Crome & Irvine, 1986).

EFFECTS OF FIRE AND DROUGHT ON FLOWERING

In the Australian Myrtaceae flowering is not enhanced by fires. In fact, the flush of vegetative growth in recovering, fire-resistant species generally inhibits flowering for several seasons (Beardsell et al., 1993). In contrast, van Wyk and Lowrey (1988) reported that in southern Africa, grassland fires promoted new growth and flowering in the rhizomatous geoxylic suffrutex *Eugenia albanensis* Sond., and these authors considered that similar effects were likely in *E. cf. mossambicensis* and *E. pusilla* N. E. Br. Cesar (1980) reported three Myrtaceae (one *Campomanesia* sp. and two undetermined Myrtaceae) among 50 species that presented some form of fire-induced flowering in central Brazilian savanna grassland. *Eugenia myrcianthes* Nied. flowers very soon after burning in the same habitat (C. Proença, pers. obs.).

Sanaiotti and Magnusson (1995) studied the effects of annual fires on the production of fleshy fruits in a Brazilian Amazonian savanna. In *Eugenia biflora* DC. and *Myrcia sylvatica* (G. Mey.) DC. fruiting was dramatically reduced after fire, but recovery was rapid with fruiting reaching 50–90% of normal levels in the first year after burning and 50–100% in the second year.

Van Wyk and Lowrey (1988) considered drought conditions a major factor in delayed flowering in southern African *Eugenia*, while Falcão et al. (1988, 1989, 1992) reported flowering periods coinciding with precipitation minima in three Amazonian species, i.e., *Eugenia stipitata*, *Myrciaria dubia*, and *Psidium acutangulum*.

BREEDING SYSTEMS

DICHOGAMY

Beardsell et al. (1993) commented that all hermaphroditic species of the Myrtaceae studied so far, except for one protogynous species of *Verticordia*, have protandrous flowers, although there may be some overlap of male and female phases providing potential for self-pollination. Intervals of days or even weeks separating male and female phases are not uncommon in the Leptospermoideae, but the potential for such conspicuous protandry is significantly reduced in the Myrtoideae where flowers are generally short-lived. Furthermore, the detection of dichogamy in the Myrtoideae is rendered more dif-

ficult by the dry nature of the stigma, which does not permit visual assessment of receptivity.

From a theoretical viewpoint it seems unlikely that temporal separation of male and female functions should be widespread but undetected among the Myrtoideae with short-lived flowers which offer only pollen as a reward. Female-phase flowers would offer nothing to reward visitors and, as Renner (1989) commented, only mimicry or deception might account for visits to such flowers. That dichogamy should co-occur with nectar production seems more likely and this does in fact appear to be the case in at least three of the four genera where the existence of dichogamy has been postulated.

Dichogamy seems most likely to occur in *Syzygium*, where many species offer nectar as a reward; interestingly, this genus includes species with relatively long-lived flowers possibly affording more scope for temporal separation of male and female functions. In the context of the Myrtoideae the flowers of *Syzygium cormiflorum*, as already mentioned, are remarkably long-lived: styles do not brown until, on average, a week after anthesis, and they are not shed until about three weeks later (Crome & Irvine, 1986). According to these authors a flower could be successfully pollinated at anthesis, but they were unable to tell whether the stigma was actually receptive on the first day or whether the pollen retained viability until the stigma matured later. Thus protandry is possible but not confirmed in this species.

The only reliable report of protandry in the Myrtoideae that we have encountered to date is that of Grifo (1992) for *Myrcianthes*. In some species of this genus the stigma remains introrsely curved until after the anthers have released much of the pollen through longitudinal slits and are leaning outwards, away from the now erect and apparently receptive stigma. Grifo (1992) also reported nectar production in *Myrcianthes*—see Attractants and Rewards below.

Peters and Vasquez (1986/87) have documented protogyny in *Myrciaria dubia*, where the stigma is exerted first and the filaments of the numerous anthers expand later. These authors stated that anthesis occurs early in the morning, that the flowers are receptive to pollination for a period of 4–5 hours, and that by the time the anthers emerge to release the pollen the stigma is no longer receptive to pollination. The method of assessment of stigma receptivity was not discussed but in the accompanying diagram the stigma appears shrivelled in the flower with erect stamens. After pollination the stamens start to wilt and the whole hypanthial cup,

with sepals, petals and stamens, abscisses on the following day, leaving only the ovary. Grifo (1992) commented that the monotypic *Amomyrtella* is also decidedly protogynous. The large peltate stigma of this species is exerted before the petals unfold (herbarium label for *Solomon 11018*).

Stylar extension post-anthesis is common in the Leptospermoideae. It appears to coincide with the onset of stigma receptivity and has been variously interpreted as a mechanism to favor outcrossing (Moncur & Boland, 1989) or as a mechanism to reduce interference from self-pollen (Lloyd & Webb, 1986; Webb & Lloyd, 1986). The phenomenon appears to be rarer in the Myrtoideae but has been reported from two species of *Syzygium*. In the flowers of *S. cormiflorum* the style expands to maximum length 4–5 days after opening and after the stamens are shed (Crome & Irvine, 1986). In contrast, in the one-day flowers of *S. lineatum*, the style reaches its full length 4 to 6 hours after anthesis, often while the anthers still have much pollen on them (Lack & Kevan, 1984).

ANDROMONOECY AND DIOECY

Andromonoecy, which is common in the Leptospermoideae (Beardsell et al., 1993), has not been detected in the Myrtoideae. Interestingly, Beardsell et al. (1993) suggested that andromonoecy in the Australian Myrtaceae (Leptospermoideae) may represent a response to soils of low fertility and to drought, allowing optimal resource allocation for reproduction. The Myrtoideae, in contrast, though tolerant of poor soils appear to be drought avoiders, reaching their maximum ecological importance (as estimated by density and/or basal area) in areas of South America where there is a combination of coolish temperatures, a steady supply of water, and a poor, weakly acidic soil (Proença, 1991).

The term cryptic dioecy has been applied to dioecious breeding systems in which one or both of the functionally unisexual morphs appear to have perfect hermaphroditic flowers, making the dioecious condition difficult to detect (Mayer & Charlesworth, 1991). In populations of most cryptically dioecious species, plants with staminate flowers (male) co-exist with apparently perfect-flowered but functionally pistillate (female) plants whose anthers produce sterile or abnormal pollen, or are indehiscent. This situation is sometimes mistaken for androdioecy, in which functionally male and functionally hermaphrodite individuals co-exist.

Nic Lughadha (1994) summarized current knowledge on dioecy in the Myrtaceae, which has until recently been considered a relatively rare phenom-

enon (van Wyk & Lowrey, 1988). In the Myrtoideae, cryptic dioecy has been reported in *Pimenta dioica* (Chapman, 1964), in *Decaspermum parviflorum* (Kevan & Lack, 1985), and in all 15 species of *Eugenia* native to South Africa (van Wyk & Lowrey, 1988). With the exception of *Pimenta dioica*, which has structurally hermaphroditic flowers in both sexes, all of these species have male flowers with greatly reduced pistils, while female flowers appear perfect but generally have fewer stamens whose anthers do not produce viable pollen. In the typically small myrtaceous flower with its many stamens, both types of cryptic dioecy (apparently hermaphrodite and apparently androdioecious) may easily be overlooked by the casual observer and are probably more common than the few literature reports suggest.

Reduced styles and abortive ovaries have been reported for *Pimenta guatemalensis* (Lundell, 1968) and for three species of *Calyptanthes*, *C. fasciculata* O. Berg (Berg, 1857), *C. longifolia* O. Berg, and *C. speciosa* Sagot (McVaugh, 1958). In the *Flora of Peru*, McVaugh (1958) also noted short styles and apparent imperfect development of the hypanthium in *Myrcia aliena* McVaugh and suggested that this species may be partially or completely dioecious. A further two imperfect flowered species are among the thirty species of *Myrcia* described as new by McVaugh (1969). *Myrcia imperfecta* McVaugh and *M. myriantha* McVaugh (both from Mount Ayanganna, Guyana) were each based on a single collection with male flowers only and no vestige of a style. McVaugh commented that this was a condition rarely noted in *Myrcia* and that its significance was unknown, though the imperfect flowers of *M. imperfecta* could be abnormal. *Myrcia almasensis* Nic Lughadha from the Pico das Almas, Brazil, was based on apparently male material with a vestigial style and brought to four the total number of putatively dioecious species of *Myrcia*. Of course the possibility that some of these collections may represent andromonoecious species cannot as yet be discounted. Interestingly, many of these putatively dioecious neotropical Myrtoideae are from high-altitude areas. Sobrevila and Arroyo (1982) have discussed the abnormally high incidence of dioecy in a Venezuelan montane cloud forest as compared to other tropical forest communities.

Classical dioecy, where female flowers lack stamens completely, is unlikely to occur in the Myrtoideae. In flowers offering pollen as a sole reward to pollinators, which is the case for most Myrtoideae, selection tends to favor female flowers which mimic male flowers by retaining stamens, even though the pollen therein may be sterile (Lloyd, 1982). A possible mechanism for the evolution of

dioecy in pollen-only taxa is outlined under Attractants and Rewards below.

Dioecy is unknown in the Australian Myrtaceae (Beardsell et al., 1993), and we consider it highly improbable that it has been extensively overlooked there. The only published example we have encountered of dioecy in the Leptospermoideae occurs in the small genus *Carpolepis*, which is endemic to New Caledonia (Dawson, 1992). *Carpolepis elegans* is dioecious and, apparently, more or less cryptically so. Male flowers include fertile stamens, a morphologically normal, but non-functional ovary, a full-length style, and a peltate stigma; female flowers are similar but the stamens are replaced by recurved staminodes whose anthers bear no pollen. The other two species of *Carpolepis* bear hermaphrodite flowers with punctiform stigmas. Dioecism has also been discovered in some species of the Myrtoideae of New Caledonia, and these are shortly to form the basis of a new genus (J. W. Dawson, pers. comm.).

The fact that dioecy is extremely rare in the Leptospermoideae yet appears to have arisen independently on at least half a dozen different occasions in the Myrtoideae can be interpreted as further evidence in support of the non-random association between dioecy and dispersal mode, which was described and discussed by Bawa (1980) and Givnish (1980, 1982). These authors argued that unisexuality is more likely to establish itself in taxa with large few-seeded animal-dispersed fruits than in taxa with other modes of dispersal. In species that produce nutrient-rich fruit an increase in female reproductive effort produces a disproportionate increase in female fitness due to selection for spatial and temporal peaks in fruit production. They consider that such an advantage to increasing female effort could, under certain circumstances, favor individuals that invest only as females or only as males.

OUTCROSSING RATES

In most Myrtoideae, especially the small-flowered species, many flowers are produced per tree per flowering day. The potential for geitonogamy would therefore seem great. However the low PERS values [Pre-emergent reproductive success, the percentage of all ovules maturing into seeds expressed as: % natural fruit set \times no. of seeds per fruit/no. of ovules per fruit, Wiens et al., 1987] typically found in the Myrtoideae (Proença & Gibbs, 1994; Nic Lughadha, unpublished data) are suggestive of predominantly outbreeding species. Electrophoretic studies have demonstrated the existence of high outcrossing rates in various species

of *Eucalyptus* and *Melaleuca* with similar flowering patterns (Phillips & Brown, 1977; Moran & Bell, 1983; Griffin et al., 1987; Butcher et al., 1992). Beardsell et al. (1993) interpreted these high levels of outcrossing in spite of ample opportunities for geitonogamy as reflecting the operation of a barrier to self-pollination such as self-incompatibility. Proença (1991) suggested that high levels of outbreeding could be maintained even in self-compatible species through flowering strategies that favor trap-lining or opportunistic behavior by pollinators. In cultivated *Psidium guajava*, a relatively low level of outcrossing of 25–41% (mean = 36%) was reported by Soubihe Sobrinho and Gurgel (1962).

SELF-INCOMPATIBILITY

Beardsell et al. (1993) considered that self-incompatibility is probably widespread in the Myrtaceae. They cited cases ranging from partial self-incompatibility to complete self-sterility with no seed production after selfing. No myrtoid examples of self-sterility were reported, but they considered it likely that the same mechanism of self-incompatibility operates throughout the Myrtaceae and acknowledged the need to examine more species in order to determine whether reduced seed-set after selfing is due to the expression of lethal recessive genes in the zygote or to a late-acting self-incompatibility system. The latter explanation was favored by Proença and Gibbs (1994) in their study of the reproductive biology of central Brazilian Myrtoideae. Of the eight species studied by these authors, three (*Blepharocalyx salicifolius*, *Campomanesia velutina*, and *Siphoneugena densiflora*) were apparently strictly self-incompatible and set no fruit when selfed. A further two species (*Myrcia linearifolia* and *Campomanesia pubescens*) exhibited partial self-incompatibility with ISI values [Index of Self-Incompatibility, expressed as the ratio of fruit set from selfed vs. crossed flowers] of 0.12 and 0.09, respectively. Self-pollen tubes were observed to penetrate ovules in all of these species and no differences were detected between self- and cross-pollinations with respect to the mean number of penetrated ovules per flower at 24, 48, or 72 hours after pollination. The time of abscission of selfed pistils varied between species from one week to one month after pollination, but rejection was synchronous within species, and no ovary enlargement was detected in crossed or selfed pistils up to the time of abscission of the latter. This represents the most detailed study of "self-incompatibility" in the Myrtoideae published to date but, as no material was fixed beyond 72 hours after pollina-

tion, we can only speculate as to the nature of the rejection mechanism in operation. More recent studies on *Gomidesia* have included fixations up to 28 days after pollination, and results obtained to date suggest that preferential outcrossing is sustained by a post-zygotic mechanism or effect (Nic Lughadha, unpublished data).

Complete self-sterility has also been reported in *Eugenia* sp. in secondary deciduous forest in Venezuela (Ruiz & Arroyo, 1978), in *Eugenia* sp. (presumably different) in montane cloud forest in Venezuela (Sobrevila & Arroyo, 1982), and in *Syzygium lineatum* in Sulawesi, Indonesia (Lack & Kevan, 1984). Bullock (1985) reported almost complete self-incompatibility in Mexican *Psidium sartorianum* Nied. (ISI 0.02). However, in none of these cases is any indication given of the timing or nature of the reproductive barriers operating after self-pollination.

Reports of self-compatibility in Myrtoideae are almost as numerous as those of self-incompatibility. Proença and Gibbs (1994) recorded three completely self-compatible species (*Eugenia dysenterica*, *Myrcia rhodosepala*, and *Psidium firmum*) that set statistically equal numbers of fruits after self- and cross-pollination. For the cultivated guava, *Psidium guajava*, self-pollination in isolated trees has been registered between 64% and 90% (Soubihe Sobrinho & Gurgel, 1962). In Peru, *Myrciaria dubia* showed 91% fruit set after geitonogamous pollination (Peters & Vasquez, 1986/87). In Venezuela, *Myrcia fallax* (Rich.) DC. showed significantly diminished fruit set after self-pollination as compared to cross-pollination; however, its ISI of 0.24 exceeded the threshold value of 0.2 arbitrarily set for self-incompatible species (Bawa, 1974; Sobrevila & Arroyo, 1982), and so this species was classed as self-compatible. *Syzygium cormiflorum* from northern Queensland also exhibited partial self-compatibility with 18–36% fertilization (estimates based on ovule enlargement) in self-pollinated flowers and 72.7–86.7% fertilization in cross-pollinated flowers (Crome & Irvine, 1986). In another northern Queensland tree species, *Syzygium tierneyanum*, bagged inflorescences set fruit in the absence of cross-pollination (Hopper, 1980). Beardsell et al. (1993) interpreted this result as demonstrating autogamy (in the sense of automatic self-pollination of a self-compatible species) but did not discuss the possibility of apomixis. Chantaranonthai and Parnell (1994) obtained similar results in a study of breeding systems of Thai species of *Syzygium*. They found that all four species studied in detail were apparently self-compatible with self-pollination appearing to enhance seed-set.

However, they further demonstrated that two of these species were actually apomictic (see below). Purseglove (1968) documented self-fertility in *Psidium guajava*. Schroeder (1947) reported results ranging from complete self-compatibility to almost complete self-incompatibility in different varieties of *Acca sellowiana* (O. Berg) Burret (as *Feijoa sellowiana* O. Berg).

APOMIXIS

Davis (1966) reported apomixis as occurring widely within the Myrtoideae. Where apomixis occurs it is generally by adventitious embryony, although there is some evidence indicating the possibility of apospory. The resulting polyembryony is discussed in more detail under Embryo and Seed Development (see below).

Rye (1979) postulated a positive correlation between the widespread occurrence of apomixis in the Myrtoideae and the high frequency of polyploidy in this group, but commented that the only specific example was *Syzygium jambos* (cited as *Eugenia jambos*). A further example is *Syzygium cumini*, which exhibits adventitious polyembryony (though apparently not consistently: Narayanaswami & Roy, 1960a; Roy & Sahai, 1962 (as *S. caryophyllifolium*); Tiwary, 1926 (as *Eugenia jambolana* Lam.); van der Pijl, 1934 (as *Eugenia cumini* (L.) Druce); Chantaranonthai & Parnell, 1994) and in which several authors reported varying levels of polyploidy (Mehra, 1976; Bir et al., 1980; Singhal & Gill, 1984; Singhal et al., 1984, 1985; Gill et al., 1989: as *E. jambolana* in each case, gametophytic counts 11, 22, and 33, sporophytic counts 22, 44, and 66). Whether this association extends to other polyembryonic members of the genus *Syzygium* and, more importantly, whether it is continued outside the genus remains to be investigated. *Luma apiculata*, the only other polyembryonic species of the Myrtoideae for which chromosome counts are available, lends no support to Rye's hypothesis as it is reported to have $n = 10$ (Titow de Tschischow, 1956), or about $2n = 22$ (Landrum, 1981). However, as there is circumstantial evidence that polyploidy may not be ubiquitous in this species, it is possible that these diploid counts may derive from non-polyembryonic material. The correlation cannot be tested further in the absence of chromosome counts for any other myrtoid genera in which polyembryony has been documented.

POLLINATION BIOLOGY

ATTRACTANTS AND REWARDS

Petals and/or stamens may act as the visual attractants in flowers of the Myrtoideae, but the sta-

mens are generally the most conspicuous structures in the open flower. Scent also appears to play a role in attraction. The odors produced are generally described as sweet but flowers of *Syzygium cormiflorum* have a faint unpleasant smell (Crome & Irvine, 1986). Grifo (1992) described the flowers of *Myrcianthes* as smelling either sweet and similar to an apple-blossom or rather sour and similar to "well-seasoned sneakers." Chantaranonthai and Parnell (1994) found that floral buds of *Syzygium jambos* and *S. megacarpum* (Craib) Rathakr. & N.C. Nair were sweetly fragrant during the period of swelling before anthesis. In southern African *Eugenia* species van Wyk and Lowrey (1988) did not discover any osmophores but found that the strong sweet odor was emitted either by the anther tissue and/or by the pollen grains.

Pollen is the principal reward available to visitors of most Myrtoideae flowers. Van Wyk and Lowrey (1988) found that the pollen of southern African *Eugenia* tested positive for lipids (in the form of oil droplets) and negative for starch. Moncur (1988) commented that sugars in pollen are pollinator rewards in *Acca sellowiana* (as *Feijoa sellowiana*). In several dioecious species, such as the southern African *Eugenia* and *Decaspermum parviflorum*, female flowers produce non-viable pollen-like material which may represent an important resource to insect pollinators (Kevan & Lack, 1985; van Wyk & Lowrey, 1988). Kevan and Lack commented that *D. parviflorum* is unusual among dioecious species in presenting pollen (and sterile pollen) as the main food reward and cited *Vitis* and *Solanum* as other examples of this phenomenon. However, pollen-only flowers also occur in other dioecious species such as *Actinidia chinensis* Planch. (Schmid, 1978), *Rosa setigera* Michx. (Kevan et al., 1990), and *Saurauia veraguasensis* Seem. (Haber & Bawa, 1984). It is noteworthy that female flowers of these species accrue neither of the major advantages proposed by Bawa (1980) for female flowers of dioecious species: they must still allocate resources to the production of stamens and sterile pollen and still run the risk of their stigmas becoming clogged with their own sterile pollen. This could be interpreted as an indication that the avoidance of inbreeding may represent a more important selective force in the maintenance of dioecy in these species than does the reallocation of reproductive resources (Mayer & Charlesworth, 1991). However, it should be borne in mind that reallocation of resources may take place on a whole-plant level, with male plants producing a more prominent floral display, more flowers, and/or more pollen per flower than female plants. This is certainly true of *D. par-*

viflorum (Kevan & Lack, 1985), and there is circumstantial evidence that it may be the case in other putatively dioecious Myrtoideae (Nic Lughadha, 1994). Givnish (1980) discussed the potential role of sexual selection in the evolution of dioecy in pollen-only taxa. Where pollen is the only reward then disproportionately many pollinators may be attracted to plants with heavy pollen loads. This advantage could drive the evolution of dioecy if male and female flowers mimic each other, as is the case in all dioecious Myrtoideae known to date (see discussion of dioecy above).

Besides the pollen and sterile pollen offered as the principal reward, *Decaspermum parviflorum* is also reported to produce minute quantities of nectar (Kevan & Lack, 1985). Most other reliable reports of nectar production that we have encountered refer to species of the genus *Syzygium*. Schmid (1972b) described an ovarian annular nectary in *S. aromaticum* (L.) Merr. & L. M. Perry, *S. jambos*, *S. malaccense*, and *S. paniculatum* and cited Werth's (1901) account of the secretion of nectar in copious amounts into the concavity formed by the depressed top of the ovary in flowers of *S. jambos* (as *Jambosa vulgaris* DC.). Crome and Irvine (1986) measured copious but variable flow of weak nectar in *S. cormiflorum*. Small quantities of nectar of rather high sugar content are produced in flowers of *S. lineatum* (as *S. syzygioides*; Lack & Kevan, 1984). Nectar production is also reported from *S. tierneyanum* (Hopper, 1980) and *S. samarangense* (Blume) Merr. & L. M. Perry (Chantaranonthai & Parnell, 1994).

Studies of genera of Myrtoideae other than *Syzygium* have generally failed to find any evidence of nectar production. Nectar is absent in flowers of southern African *Eugenia* species (van Wyk & Lowrey, 1988) and, apparently, in most South American Myrtoideae (Landrum, 1986; Proença & Gibbs, 1994; Nic Lughadha, unpublished data). Exceptions include the report by Pirani and Cortopassi-Laurino (1993) of bees collecting pollen and nectar from flowers of *Plinia glomerata* (O. Berg) Amshoff and that of Peters and Vasquez (1986/87) on nectar production in *Myrciaria dubia*. The other notable exception is the genus *Myrcianthes*, in which sweet-tasting nectar is secreted at the base of the staminal disk (Grifo, 1992). Grifo's descriptions of visitor behavior indicate that nectar is the principal reward offered by these species. Small insects may approach the flowers and feed on the nectar while entirely avoiding the numerous stamens, but larger insects become covered with pollen as they brush the anthers in search of nectar.

Nectar is widespread in the Leptospermoideae, and the nectar-producing *Chamelaucium* group

emerged as sister to the Myrtoideae in cladistic analyses by both Johnson and Briggs (1984) and Grifo (1992) (along with the *Leptospermum* group in the former analysis). Grifo's (1992) cladistic analysis also indicated that *Myrcianthes* is "much more closely related to *Syzygium* than previously supposed" and that these genera are basal to the Eugeniinae in the Neotropics. We can therefore hypothesize that nectar production is basal in the Myrtaceae with the numerous pollen-only genera of the Myrtoideae arising as a result of secondary loss(es) of this facility. Renner (1989) has proposed a similar scenario to explain the distribution of nectar production among the neotropical melastomes. Her observation that the Melastomataceae that offer nectar are pollinated by a broader range of pollinator classes than the pollen-only species seems also to hold true for the Myrtaceae on the basis of the evidence available to date.

The role of the secretory cavity at the apex of the anther connective does not appear to have been investigated in any member of the Myrtoideae. In *Thryptomene calycina* (Lindl.) Stapf, a member of the *Chamelaucium* alliance (Leptospermoideae s.l.), Beardsell et al. (1989) demonstrated that the anther connective glands secrete a lipid-rich fluid which solidifies and serves as a food reward for pollinating insects. Although a similar role is possible for the anther connective glands of the Myrtoideae it seems unlikely that any visitor small enough to be attracted to the minute quantities of secretion that these glands might afford would contact the stigma regularly while collecting. Renner (1989) discussed a comparable paradox offered by the staminal glands of *Mouriri* (Memecylaceae) and noted Morley's (1976) suggestion that these glands may be involved in odor production. Van Wyk and Lowrey's (1988) observations on fragrant anthers and pollen in southern African *Eugenia* represent the only evidence we have encountered to support the hypothesis of an odor production role for the anther connective glands in the Myrtoideae. Of course, another possibility is that these structures serve no function in the flowers of the Myrtoideae and are simply vestigial remnants of an organ which is more or less ubiquitous in the Myrtaceae. The scattered examples of species whose anthers lack secretory cavities undoubtedly represent secondary losses of this feature.

The role of petals as an attractant and reward to visitors to *Acca* and *Myrrhinium* is discussed under Bird Pollination below.

BEE POLLINATION

Bees (Apoidea) appear to be the most common pollinators of Myrtoideae, as they are of Myrtaceae

as a whole. There is a strong association between the Myrtaceae and the short-tongued Colletidae, which are considered to be the most primitive flower-visiting bees (Michener, 1979). This relationship is most notable and best documented in Australia where nearly half of the bee species belong to the Colletidae and most of these are restricted to or collect pollen primarily from flowers of Myrtaceae (Armstrong, 1979). These include *Eugenia* and *Syzygium* as well as numerous non-myrtoid genera. Bees reported to collect pollen from *Eugenia* and/or *Syzygium* include *Euryglossina* and *Hylaeus* (Colletidae) as well as *Homalictus* and *Lasioglossum* (Halictidae) (Michener, 1965). When current taxonomic concepts are applied, most of these records are referable to the genus *Syzygium*; only one species of *Eugenia* s. str. occurs in Australia (Hyland, 1983).

Proença and Gibbs (1994) suggested that the Myrtaceae–Colletidae association, so striking in Australia, probably exists to some extent in the Neotropics. They cited two neotropical examples of this association, viz., rapid pre-dawn pollen removal from *Eugenia salamensis* by *Ptiloglossa* spp. (Colletidae: Diphaglossinae) in Costa Rica (Frankie et al., 1983) and pollination of *Siphoneugena densiflora* by *Ptiloglossa* sp. in central Brazil (Proença, 1992). Colletidae are not particularly common in the Neotropics: e.g., in central Brazil, where the Proença and Gibbs study was carried out, only 5% of bee species are Colletidae (A. Raw, unpublished list based on 12,000 collections). Therefore one could argue that such reports are unlikely in the absence of some degree of association. However, a careful compilation of 33 reports of bee visitation in neotropical Myrtoideae (Table 2) showed that most registered visits are by Apidae: Meliponinae (14), followed by Apidae: Bombinae (9), Halictidae (4), Anthophoridae (4), Colletidae (2). In defense of the neotropical Myrtaceae–Colletidae association, it should be noted that both reports were of pre-dawn visitation, so that this phenomenon could be widespread but largely overlooked in studies based purely on diurnal observations.

The first report of buzz-pollination in the Myrtaceae was published by Proença (1992). She described buzz-pollination in *Siphoneugena densiflora* by *Ptiloglossa* sp., in *Myrcia torta* DC. (as *M. dictiophylla* (O. Berg) J. R. Mattos & D. Legrand) by *Augochloropsis?* sp. (Halictidae), and in *Myrcia rhodosepala* and *Blepharocalyx salicifolius* by *Bombus* spp. (Apidae: Bombinae). *Bombus* spp. (including *B. atratus* and *B. morio*) were considered the principal pollinators of a further five species of central Brazilian Myrtaceae (*Campomanesia pubescens*, *C.*

Table 2. Species of neotropical Myrtoideae with presumed pollinators or insect visitors to flowers.

Species	Visitors	Behavior	Reference
<i>Blepharocalyx salicifolius</i>	Apidae: Bombinae Apidae: Meliponinae Halictidae	"visitors"	Proença & Gibbs (1994)
<i>Campomanesia pubescens</i>	Apidae: Bombinae	"visitors"	Proença & Gibbs (1994)
<i>Campomanesia velutina</i>	Apidae: Bombinae	"visitors"	Proença & Gibbs (1994)
<i>Eugenia dysenterica</i>	Apidae: Bombinae Apidae: Meliponinae	"visitors"	Proença & Gibbs (1994)
<i>Eugenia salamensis</i>	Colletidae	"foraging"	Frankie et al. (1983)
<i>Eugenia stipitata</i>	Apidae: Meliponinae	"visiting"	Falcão et al. (1988)
<i>Eugenia</i> sp. 1	Apidae: Meliponinae	"aggressive behavior"	Roubik (1989)
<i>Eugenia</i> sp. 2	Halictidae	"visits"	Ruiz & Arroyo (1978)
<i>Eugenia</i> spp.	Apidae: Meliponinae	"collect pollen"	Absy & Kerr (1977)
<i>Myrcia linearifolia</i>	Apidae: Bombinae	"visitors"	Proença & Gibbs (1994)
<i>Myrcia rhodosepala</i>	Apidae: Bombinae Anthophoridae: Xylocopinae	"pollinators"	Proença & Gibbs (1994)
<i>Myrcia torta</i>	Halictidae ?	"pollinators"	Proença & Gibbs (1994)
<i>Myrcia</i> sp.	Apidae: Meliponinae	"pollen in honey"	Vit & D'Albore (1994)
<i>Myrciaria dubia</i> 1	Apidae: Meliponinae	"visiting"	Falcão et al. (1989)
<i>Myrciaria dubia</i> 2	Apidae: Meliponinae	"pollinators"	Peters & Vasquez (1986/87)
<i>Pimenta dioica</i>	Anthophoridae: Xylocopinae Anthophoridae: Anthophorinae Halictidae	"visiting"	Chapman (1965)
<i>Plinia cauliflora</i>	Apidae: Meliponinae	"intensive exploitation"	Guibu et al. (1988)
<i>Plinia glomerata</i>	Apidae: Bombinae Apidae: Meliponinae	"foraging"	Pirani & Cortopassi- Laurini (1993)
<i>Psidium acutangulum</i>	Apidae: Meliponinae	"visiting"	Falcão et al. (1992)
<i>Psidium firmum</i>	Anthophoridae: Xylocopinae Apidae: Bombinae	"presumptive pollinator"	Proença & Gibbs (1994)
<i>Psidium guajava</i> 1	Apidae: Meliponinae Apidae: Bombinae	"foraging"	Camillo & Garófalo (1989)
<i>Psidium guajava</i> 2	Apidae: Meliponinae	"intensive exploitation"	Guibu et al. (1988)
<i>Siphoneugena densiflora</i>	Colletidae	"presumptive pollinator"	Proença (1992)
Myrtaceae indet. spp.	Apidae: Meliponinae	"pollen in honey"	Vit & D'Albore (1994)

Note. Visits by honeybees, introduced to the Neotropics, are excluded from this table.

velutina, *Eugenia dysenterica*, *Myrcia linearifolia*, and *Psidium firmum*), but no buzzing behavior was noted during observation of these species. The same species of *Bombus* exhibited a preference for *Psidium guajava* in secondary vegetation in southeastern Brazil (Camillo & Garófalo, 1989). *Bombus* spp. were reported to collect pollen and nectar from *Plinia glomerata* in São Paulo (Pirani & Cortopassi-Laurino, 1993). Visits by *Melipona quadrifasciata*, *Tetragonisca angustulata* (both Apidae: Meliponinae), and *Apis mellifera* were also recorded. Guibu et al. (1988) documented intensive exploi-

tation of Myrtaceae by *Melipona quadrifasciata*. They listed *Psidium guajava* s.l. and *Plinia cauliflora* (Mart.) Kausel s.l. (as *Myrciaria cauliflora* (Mart.) O. Berg s.l.) among the species visited by these bees in São Paulo, Brazil.

Other species of the bee genus *Melipona* may be important pollinators of Myrtaceae in Amazonian Brazil. *Melipona rufiventris* and *M. seminigra* collected pollen of *Eugenia* spp. and other unidentified Myrtaceae near Manaus (Absy & Kerr, 1977; Absy et al., 1980). In the same area Falcão et al. (1988, 1989, 1992) recorded *Melipona lateralis* and

M. pseudicentris visiting cultivated *Eugenia stipitata*, *Myrciaria dubia*, and *Psidium acutangulum*. In the nearby Reserva Ducke, Roubik (1989) observed aggressive behavior of several species of *Trigona* (Meliponinae) on *Eugenia* sp. In Peru *Myrciaria dubia* is commonly pollinated by *Melipona fuscopilara* and *Trigona postica* (Peters & Vasquez, 1986/87). A recent study of pollen spectra in the honey of 48 species of *Melipona* in Venezuela (Vit & D'Albore, 1994) provides additional evidence of the importance of Myrtaceae to these bees: Myrtaceae spp. and *Myrcia* sp. were respectively the fifth and eighth most common pollen types in a list of 13. Ruiz and Arroyo (1978) reported visits to a Venezuelan *Eugenia* sp. by *Augochloropsis fulvofimbriata* (Halictidae) and by *Apis mellifera* and *Trigona testaceicornis* (Apidae).

Chapman (1965) saw solitary bees belonging to the genera *Ceratina* (Anthophoridae, Xylocopinae), *Exomalopsis* (Anthophoridae, Anthophorinae), and *Halictus* (Halictidae), as well as honeybees, visiting flowers of *Pimenta dioica* for pollen in Jamaica.

In a population of *Decaspermum parviflorum* in a forest clearing in Indonesia, Kevan and Lack (1985) recorded vigorous pollen collection during a 45-minute peak period by a variety of bees, mostly *Apis dorsata* (Apidae: Apiinae) and *Nomia* spp. (Halictidae: Nomiinae). *Nomia* and *Trigona* continued to glean during the rest of the day and perfunctory visits by *Xylocopa* spp. were also reported. In a nearby forest *Syzygium lineatum* (as *Syzygium syzygioides* and subsequently corrected) was visited sparingly and mainly for nectar (Lack & Kevan, 1984). Another study notable for the paucity of potential pollen vectors was that of van Wyk and Lowrey (1988). These authors provisionally considered that the 15 southern African species of *Eugenia* studied might be bee-pollinated, as honeybees were observed visiting *Eugenia* spp. in Pretoria and were also active in natural populations of *Eugenia capensis* Harv.

BIRD POLLINATION

Bird pollination appears to be much less frequent in the Myrtoideae than in the Leptospermoideae. Ford et al. (1979) reported six species of birds visiting three species of *Syzygium* in Australia, but in no case was a bird actually seen to be carrying pollen. Honeyeaters were reported as the most commonly observed vertebrate visitors to flowers of *Syzygium cormiflorum* and *S. tierneyanum* in Australia (Hopper, 1980; Crome & Irvine, 1986). Hopper (1980) suggested that honeyeaters may be the most important pollinators of *S. tierneyanum* but

acknowledged that the role of bats was neglected in his study. Crome and Irvine (1986) demonstrated experimentally that in *S. cormiflorum* birds were far less effective pollinators than bats, accounting for less than 25% of all successful pollinations. Both of these species have white or cream flowers, but Ford et al. (1979) noted a tendency for red stamens among large-flowered, bird-pollinated Australian Myrtaceae in general (mostly Leptospermoideae).

Two small neotropical myrtoid genera, *Acca* and *Myrrhinium*, have stiff red stamens reminiscent of those of many Australasian bird-pollinated Myrtaceae. Landrum (1986) noted that there is no nectar in the fresh flowers of *Acca sellowiana* and that in both genera the petals change color and become sweet and juicy just as the anthers dehisce. There are various reports of visiting birds eating the petals of *Acca sellowiana* (Kiaerskov, 1893; Knuth, 1906; McGregor, 1976; Vogel et al., 1984). In view of their isolated position within the Myrtoideae, Landrum (1986) hypothesized that the use of petals as an attractant in these two closely related genera (which he called the *Myrrhinium* complex) is very ancient. Schroeder (1947), however, observed extensive bee visitation in *Acca sellowiana* cultivated in California and found that flowers so visited set fruit ca. 16 times as well as flowers protected from visitation. Free (1993) also reported that bees are frequent visitors to the flowers of this species and assumed that they were responsible for most of the pollinations. In *Myrrhinium atropurpureum* Schott recently opened flowers have deep wine-red petals with a normal petal texture, crinkled filaments, and closed anthers; putatively receptive flowers have inflated, very pale lavender petals, stiff filaments, and dehisced anthers; the pale petals provide a dramatic contrast to the rest of the inflorescence, which is a uniform deep wine red, even to the axes, and the petal texture is unlike that of any other flower known to us, aerenchyma-rich, resembling the hollow structure of certain rubiaceous fruits such as *Coccocypselum* (C. Proença, pers. obs.). It seems likely that *Acca* and *Myrrhinium* evolved under selection for bird pollination (perhaps in areas with an impoverished bee fauna) without totally losing their adaptations to bee pollination, so that in cultivation *Acca sellowiana* at least still responds to bee pollination.

MAMMAL POLLINATION

Long-tailed pygmy possums (*Cercartetus caudatus*) feed on *Syzygium cormiflorum* in northern Queensland (Hopper, 1980). Beardsell et al. (1993) suggested that the cauliflorous flowering of several

Syzygium species might facilitate access to the flowers by larger marsupials, which move up and down the trunks and larger branches. These authors also stressed that bats, being nocturnal and not easily studied, might be more significant pollinators of some Myrtaceae than had been thought previously. *Syconycteris australis* (Queensland blossom bat) appeared to be one of the minor pollinators of the night-flowering rainforest tree *Syzygium tierneyanum* (Hopper, 1980) and also made nocturnal visits to the flowers of the cauliflorous *S. cormiflorum* (Crome & Irvine, 1986) as did *Macroglossus lagochilus*, another small blossom bat. In *S. cormiflorum* flowers open at any time of the day or night, but bats were the single most important pollinators, although visits by birds to the flowers were more frequent and more numerous. Start and Marshall (1976) reported the bats *Eonycteris spelaea* and *Macroglossus minimus* feeding on *S. malaccense* in West Malaysia.

WIND POLLINATION

Grifo (1992) considered wind-pollination possible but unlikely in *Myrcianthes*. Peters and Vasquez (1986/87) mentioned the possibility of wind-pollination in *Myrciaria dubia* and Moncur (1988) the same for *Acca sellowiana* (as *Feijoa sellowiana*), but in both of these studies bees were considered to be the most important pollinating agents.

FRUITS

FRUIT CHARACTERISTICS AND DISPERSAL AGENTS

The typical fruit of the Myrtoideae is a fleshy single-seeded, usually orange, red, or black berry, and the Myrtoideae have long been characterized as a fleshy-fruited subfamily or tribe. However, semi-dry to dry berries (i.e., leathery or pithy) have also been recorded, especially in *Eugenia* and related genera. Drupaceous fruits are reported for *Myrtella* and *Stereocaryum*. Subdrupaceous fruits, with variable levels of woodiness of the endocarp, are found in some species of *Eugenia* s.l., *Rhodomyrtus* (Schmid, 1980), and in *Acmena* (Hartley & Craven, 1977). Drupoid fruits with 1–3 pyrenes occur in *Eugenia* and *Hexachlamys* (Berg, 1857; Rotman, 1982). A very specialized “drupoid” fruit occurs in *Campomanesia*. It may be considered drupoid in that the single seeds developing in each of the locules adhere to the endocarp, as in a true drupoid fruit, but it differs in the texture of the endocarp, which can be woody or merely glandular-verrucose, simulating a false seed-coat (Landrum, 1982). The more primitive subtribe Myrtinae in-

cludes many species that have green or yellow, several- to many-seeded fruits.

Our knowledge of dispersal agents is mainly based on deductions from fruit morphology; few actual dispersal events have been reported. Fleshy perigynia have clearly evolved in association with zoochory. Briggs and Johnson (1979) highlighted two common secondary developments that may occur independently or in conjunction, viz., increase in fruit size and reduction in seed number. Proença (1991) suggested that single-seeded fruits, i.e., “packaging each seed separately,” would enable the plant to abort inferior zygotes on an individual basis and to mature fruits at different rates, thus permitting more dispersal events for the same number of seeds.

Various dispersal mechanisms have been suggested for many-seeded fruits. Landrum (1986) considered that most species of *Campomanesia* best fit the mammal dispersed syndrome as defined by Janson (1983) based on an Amazon rainforest community, but Snow (1981) registered *Campomanesia* as forming part of the diet of specialized frugivorous birds. Motta Júnior et al. (1994) reported that *Dusicyon thous*, a small nocturnal Canidae, feeds on fruits of *Psidium* sp., *Campomanesia* sp., and *Plinia cauliflora* (as *Myrciaria cauliflora*). Seeds of *Campomanesia* sp. recovered from scats germinated successfully both *in situ* and in the laboratory, indicating that this small mammal is a potentially effective dispersal agent. The genus *Psidium* is cited by Snow (1981) as having fruits that form part of the diet of specialized frugivorous birds, but *Psidium firmum* is apparently consumed by small rodents (Proença, 1991). Evidence to this effect included a gnawed-through peduncle of an unripe fruit, marks of superficial bites on unripe fruit, ripe fruit torn open and the flesh partly eaten, and nearby scats which were identified as pertaining to *Rhipidomys* or *Oryzomys*. Cultivated *Psidium guajava* is eaten by parrots (M. A. S. Alves, pers. comm.), other birds (Advani, 1981), and bats (Funmilayo, 1980; Advani, 1982). Other multi-seeded fruits mentioned by Snow (1981) include those of *Decaspermum* and *Rhodamnia*, which are exploited by specialized frugivorous birds, and *Calycolpus*, exploited by specialized and unspecialized frugivorous birds. Kevan and Lack (1985) observed mistletoe-birds (Dicaeidae) feeding on the fruits of *Decaspermum parviflorum* and discussed bird dispersal in this dioecious species in relation to the selective pressure for the production of energy-rich fruits. Ant-dispersal by *Messor minor* (André) has recently been reported for *Myrtus communis*, the

seeds of which bear elaiosomes (Aronne & Wilcock, 1994)

Johnson and Briggs (1984) suggested that in diverse lines of Myrtaceae, fruits with large, single seeds seem to be adapted to vertebrate dispersal in tropical forest. In the large genus *Syzygium*, one-seeded fruits are the norm, but mature fruits from different species may differ in diameter by an order of magnitude (Hyland, 1983). K. Fischer (pers. comm.) compared the morphology and nutritional and secondary chemistry of fruits of New Guinean species of *Syzygium* eaten by birds and by bats. In the species of *Syzygium* studied by her, fruits eaten by bats were both longer and wider than those consumed by birds but did not differ in nutrient composition or secondary chemistry. Among 16 wild fruits edible to man that were studied in Malawi, *Syzygium guineense* Guill. & Perry had the highest levels of iron and magnesium (Saka & Msonthi, 1994). Beardsell et al. (1993) noted that in many species of *Syzygium* the infructescences are borne at some distance from the tips of the branches thus allowing larger animals access to the fruits. They cited the extreme case of *Syzygium cormiflorum*, the berries of which develop on the main trunk and larger branches, and suggested that this arrangement enables larger marsupials to eat the fruits during tree to tree movements. Fruits of a cauliflorous species of *Myrciaria* are eaten by bats (Semir, 1984). *Eugenia* s.l. is cited as consumed by unspecialized frugivorous birds (Snow, 1981). Two unidentified species of *Eugenia* s. str. from Costa Rica are eaten by *Pharomachus mocinno* (Trogonidae) and by *Aulacorhynchus prasinus* (Rhamphastidae), respectively (Wheelwright et al., 1984). Fruits of *Eugenia puniceifolia* (Kunth) DC. are probably consumed by pheasant-like Tinamidae in central Brazil, and *Siphoneugena densiflora* fruits are eaten by *Miyarchus swansonii* (Tyrannidae), an opportunistic fly-catcher, and by other birds (Proença, 1990). Fruits of *Myrcia torta* DC. (as *Myrcia dictiophylla*) are eaten by *Neothraups fasciata* (Emberizidae), a generalist low-foraging tanager (Alves, 1992). Observations of *Blepharocalyx salicifolius* revealed that the fruits are swallowed whole by migratory *Elaenia chiriquensis* and *Tyrannus melancholicus* (both Tyrannidae) and by resident *Neothraups fasciata* (Emberizidae), all opportunistic frugivores that also feed on insects (Paes, 1993). Snow (1981) listed *Acmena*, *Eugenia*, *Myrcia*, and *Syzygium* as forming part of the diet of specialized frugivorous birds, while fruits of *Eugenia* and *Myrcia* are also exploited by non-specialized birds. He commented that while at least 13 genera of Myrtoideae provide fruits that are eaten by frugivorous birds, special-

ized and unspecialized, none seems to provide the staple diet of any frugivorous bird. In this respect the Myrtoideae resemble the Euphorbiaceae but differ from the Lauraceae, Burseraceae, and Palmae. Grifo (1992) saw monkeys of the genus *Alouatta* consuming the fruits of *Myrcianthes pungens* in Corrientes, Argentina. However, her observations suggested that the fruits, including the seeds, were chewed, thus considerably reducing the possibility that the monkeys were agents of dispersal.

OVULE-SEED RATIOS AND REPRODUCTIVE CAPACITY

In the fruits of most Myrtoideae, including the many-seeded ones, the number of mature seeds is much smaller than the original number of ovules in the ovary from which the fruit is derived. Even in genera in which the ovule number is reduced to two in each of two (or three) locules, most ovules do not develop into mature seeds. This superfluity of ovules may simply represent a relictual situation, with these species being derived from taxa in which most or all ovules within the ovary would have matured into seeds (Caspar & Wiens, 1981). For example, Landrum (1981) envisaged an ancestor of *Myrceugenia* that developed all or nearly all its ovules into seeds while in present-day species few ovules develop into seeds. Alternatively, the superfluous ovules may provide scope for the exercise of female choice (Stephenson & Bertin, 1983) and/or allow for the wastage of ovules inherent in a post-zygotic "self-incompatibility" system. In the dioecious *Pimenta dioica* (and the putatively dioecious *P. guatemalensis*) the number of ovules scarcely exceeds the number of seeds per fruit (Landrum, 1986). We suggest that in these species there is no need for superfluous ovules, since all pollen tubes must originate from non-self pollen.

In the Australian Myrtaceae (largely Leptospermoideae), Rye and James (1992) identified reduction in ovule numbers and competitive selection among fertilized ovules as mechanisms leading to reduction in seed number. These trends were interpreted as the result, in part at least, of selection for larger seed size. In addition, they found that plant size is positively correlated with ovule number and seed set, and that the effects of all these factors tended to reinforce each other in determining the net reproductive capacity of the species.

Another factor that has been linked to reproductive capacity is chromosome number. Rye and James (1992) found that high reproductive capacity is associated with high dysploid chromosome numbers in four genera including *Eugenia*.

EMBRYO AND SEED DEVELOPMENT

EMBRYO DEVELOPMENT

The Myrtoideae apparently follow the onagrad pattern of embryo development but, as in the Myrtaceae as a whole, the process has scarcely been studied. The dearth of information in this area is acute, even in the context of our rudimentary knowledge of Myrtoideae biology in general, and may be attributable to the extreme difficulties experienced in fixation for histological studies in the family (Mauritzon, 1939; Davis, 1968; Beardsell et al., 1989, 1993).

SEED-COAT

Beardsell et al. (1993) considered a seed-coat formed from both integuments as "a feature of all Myrtaceae so far examined." While this may summarize the situation in the Leptospermoideae it is far from true with respect to the Myrtoideae. Van Wyk and Botha (1984) reported testa formation from the outer integument only in some southern African *Eugenia* species and a pachychalazal seed-coat in others. Narayanaswami and Roy (1960b) described the testa in *Psidium guajava* (and in *P. cujavillus* Burm. f., now considered synonymous) as being formed from the outer integument only. The seed-coat appears to be entirely absent in *Acmena*, *Acmenosperma*, and *Waterhousea* (Hartley & Craven, 1977; Hyland, 1983).

McVaugh (1968) indicated that the testa varied in thickness from group to group in the neotropical Myrtoideae and may be membranous, leathery, cartilaginous, or bony. Where the seed-coat is hard (i.e., in most Myrtinae apart from Landrum's *Campomanesia* complex), an operculum in the seed-coat, located directly over the basal end of the hypocotyl, allows the embryo to emerge. Landrum and Stevenson (1986) detected a strong correlation between seed-coat texture and embryo structure but admitted the possibility that changes in embryo morphology naturally follow changes in seed-coat texture. Whatever the thickness, the testa is usually quite smooth and unsculptured.

In *Campomanesia* the thick glandular locule wall adheres to the delicate membranous testa of the single seed maturing inside the locule, as described above. The locule wall thus serves as a false seed-coat, to which Landrum (1982) attributed a protective function, hypothesizing that frugivorous birds or mammals would tear apart the fruits without biting into the glandular turpentine-smelling walls. Some field observations support this theory, as partially eaten fruits were found to have the locules

intact (Landrum, 1986) but, as discussed above, some seeds are clearly ingested by small mammals (Motta Júnior et al., 1994). Proença (1991) suggested a possible co-adaptive role for the pseudotesta, interpreting it as a defense to prevent developing larvae of Tephritidae flies from migrating from infected to healthy locules. The situation in *Campomanesia*, where each locule harbors a single developing embryo, was compared to that in a species of *Berberis* in which high mortality of Tephritidae larvae was found to occur in single-seeded fruits when compared to several-seeded fruits (Herrera, 1984). Tephritidae are notorious predators of myrtaceous fruit crops (Malavasi & Morgante, 1980; Morgante & Malavasi, 1981; Tan & Lee, 1982; Burk, 1983).

EMBRYO STRUCTURE

Embryo structure has been considered fundamental in the classification of the Myrtoideae since the time of De Candolle (1828). He distinguished three basic embryo types commonly referred to as eugenoid (with thick, fleshy cotyledons and a relatively insignificant hypocotyl), myrcioid (with leafy cotyledons that are much broader than the hypocotyl), and myrtoid/pimentoid (with a well-developed hypocotyl and relatively small, narrow cotyledons). Although most subsequent authors have used these differences as the basis for their classifications, little attention has been paid to the biological significance of these structures. One notable exception is the discussion by Landrum and Stevenson (1986) in which the various embryo types are interpreted as different responses to the same selective pressure for increased food storage in the embryo. Essential oil-secreting schizogenous glands occur in the embryos of *Pimenta racemosa* (P. Miller) J. W. Moore (as *Myrcia acris* DC.), *Luma apiculata* (as *Myrceugenia apiculata*), *Myrceugenia glaucescens* (Cambess.) D. Legrand & Kausel (as *Eugenia glaucescens* Cambess.), *Myrcianthes pungens* (as *Eugenia pungens*), and *Eugenia discolor* DC. and are absent from *Myrtus* sp., *Psidium*, *Acca* (as *Feijoa*), and *Eugenia uniflora* (as *Stenocalyx michelii*) (Petit, 1908). In a study of southern African *Eugenia*, four species had conspicuous glands and five species were described as "apparently eglandular but usually with a few obscure glands mainly associated with the radicular protuberance" (van Wyk, 1980). Hyland (1983) recorded oil glands in the embryos of 4 out of ca. 50 species of Australian *Syzygium* studied, i.e., *S. macilwraithianum* B. Hyland, *S. sayeri* (F. Muell.) B. Hyland, *S. velae* B. Hyland, and *S. wilsonii* B. Hyland. In

the Leptospermoideae the embryo lacks oil glands (Petit, 1908).

ENDOSPERM

The endosperm is nuclear and is generally described as being digested by the developing embryo and therefore absent from the mature seeds (Tobe & Raven, 1983). However, studies by Petit (1908, cited in van Wyk & Botha, 1984) have shown that traces of endosperm are present in many myrtaeous seeds including those of the genera *Acca* (as *Feijoa*), *Myrtus*, and *Psidium* (all Myrtoideae). Van Wyk and Botha (1984) reported the presence of endosperm in mature seeds of some species of southern African *Eugenia*. They suggested that variation in the amount of endosperm formed in the young seed may be of taxonomic importance, whereas the quantity of endosperm that remains in mature seeds is variable within species and therefore less likely to prove taxonomically significant.

POLYEMBRYONY

Tobe and Raven (1983) described polyembryony as usual in *Syzygium* but our literature survey suggests that, though frequent, it is by no means the norm in this genus. The earliest reports are by Tiwary (1926), who concluded that all (six) of the species of *Syzygium* (reported as *Eugenia*) examined by him showed "the existence of some kind of polyembryony." However, as he interpreted early bifurcation of the plumule as evidence of polyembryony, he may have overestimated the frequency of this latter phenomenon within the genus. In only two of the species he examined (*S. cumini* and *S. jambos*, as *Eugenia jambolana* and *E. jambos*, respectively) was the presence of more than one embryo in the seed actually demonstrated.

Subsequent studies have confirmed the existence of polyembryony in *Syzygium jambos*, disputed its occurrence in *S. cumini* (van der Pijl, 1934; Henderson, 1949; Roy, 1953; Chantaranonthai & Parnell, 1994) and in general indicated that the condition was far from ubiquitous in the genus. Van der Pijl (1934) reported polyembryony in *S. aqueum* (Burm. f.) Alston (as *Eugenia aquea* Burm.f.), *S. jambos* (as *E. jambos*), *S. javanicum* Miq. (as *E. javanica* Lam.), and *S. malaccense* (as *E. malaccensis*), but found no evidence for polyembryony in *S. cumini* (as *E. cumini*) on the basis of the examination of specimens of this species from four different localities and fruits obtained from the local market. Henderson (1949) found polyembryony in "some species" of the 138 in the genus *Eugenia* s.l. in Malaya, and Merrill and Perry

(1938) reported that of the 45 species of *Syzygium* known from China, 5 are regularly polyembryonic (*S. jambos*, *S. buxifolium* Hook. & Arn., *S. megacarpum* (as *S. latilimum* (Merr.) Merr. & L. M. Perry), *S. forrestii* Merr. & L. M. Perry, and *S. hancei* Merr. & L. M. Perry). Hyland (1983) described ca. 50 species of *Syzygium* occurring in Australia and recorded consistent polyembryony in *Syzygium paniculatum* and the presence of "two-seeded fruits" in *S. aqueum* (polyembryony? see *S. aqueum* above). Chantaranonthai and Parnell (1994) found no evidence of polyembryony in *S. cumini*, nor in *S. megacarpum* or *S. formosum*, but confirmed the existence of polyembryony in *S. jambos* and *S. malaccense* and reported production of 2–6 seedlings from 1–3-seeded fruit in *S. siamense* (Craib) P. Chantaranonthai & J. Parn. We concur with van Wyk and Botha's (1984) conclusion that most reports of polyembryony in *Eugenia* are probably referable to the genus *Syzygium*.

Johnson (1936) counted 2–22 embryos in seeds of *Luma apiculata* (as *Eugenia hookeri* Steud.). However, Landrum (1986) revised *Luma apiculata* and, although he had obviously dissected seeds and examined embryos, did not mention the occurrence of polyembryony. Thus we may infer that polyembryony is not constant in this species.

Gurgel and Soubihe Sobrinho's (1951) study of myrtaceous fruit-bearing trees in Brazil is one of the most complete studies of polyembryony in the Myrtoideae to date. Sixteen species were investigated, representing five genera native to Brazil plus *Syzygium*, which is introduced and widely cultivated. The following species were found to be consistently monoembryonic: *Campomanesia* sp. (as *Myrtus mucronata* Cambess.), *Psidium guajava*, *Psidium guineense* (as *Psidium araca* Raddi), *Eugenia uniflora*, *Eugenia tomentosa* Cambess., *Eugenia uvalha* Cambess., *Eugenia myrcianthes* (as *Myrcianthes edulis* O. Berg), *Eugenia brasiliensis* Lam., *Eugenia lucescens* Nied. (as *Phyllocalyx luschnathianus* O. Berg), and *Gomidesia reticulata* O. Berg.

Gurgel and Soubihe Sobrinho (1951) found a high percentage of polyembryony in *Syzygium malaccensis* (66–97%) and *Syzygium cumini* (76–95%). One to eleven embryos were reported per seed. Repeated sampling of these species in successive years suggested the existence of a phenetic as well as a genetic component to the level of polyembryony. A low to medium percentage of polyembryony (33–70%), with one to five embryos reported per seed, was found in the following native Brazilian species: *Plinia cauliflora* (as *Myrciaria cauliflora*), *Plinia trunciflora* (O. Berg) Kausel (as

Myrciaria trunciflora O. Berg), and *Plinia edulis* (Vell.) Sobral (as *Eugenia edulis* Vell.), as well as a species cited as *Myrciaria trunciflora*, which Mattos (1989), based on the common name, claimed to be *Myrciaria coronata* Mattos. Sobral (1993) excluded this species from *Myrciaria* in his recent revision of that genus and stated that it is a *Plinia*. Rotman (1982) registered consistent polyembryony in *Guapurium peruvianum* (possibly = *Plinia*) but registered no polyembryony in *Plinia trunciflora*. Thus all low to medium polyembryonic species may be members of genus *Plinia*. Traub (1939) had already noted that polyembryony was usual in *Plinia cauliflora* (as *Myrciaria cauliflora*) cultivated in Florida.

Observations on the origin of the embryos in polyembryonic seeds are few and disparate. Tiwary (1926) reported embryos originating from the egg cell (presumably sexual), from the synergids and from the nucellus in *S. cumini* (as *Eugenia jambolana*). Narayanaswami and Roy (1960a) and Roy and Sahai (1962) also studied *S. cumini*, and the latter authors found that the fertilized egg degenerates along with the synergids. The upper half of the nucellus becomes proliferative and produces several embryos, one or more of which may survive, producing mono- or polyembryonic seeds in this species. Roy and Sahai (1962) also noted the occasional production of supernumerary embryo-sacs (by apospory or by the activity of more than one archesporial cell) but reported that ovules in which this occurs eventually degenerate. The multiple embryos in seeds of *S. jambos* are also of nucellar origin (van der Pijl, 1934), and Johnson (1936) tentatively suggested a nucellar origin for the embryos of *Luma apiculata* (as *Eugenia hookeri*). Gurgel and Soubihe Sobrinho (1951) confirmed that in *S. jambos* the sexual embryo often dies immediately after fertilization. However, they considered the adventitious embryos to be derived from the inner integument. Van der Pijl (1934) reported an integumentary origin for the multiple embryos of *Syzygium malaccense* (as *E. malaccensis*).

REGENERATION FROM SEED

Beardsell et al. (1993) highlighted the lack of published data on the regeneration of the Myrtoideae of the tropical forests. They suggested that germination requires breakdown of the pericarp by weathering or ingestion by animals including birds, and reported that some species of *Syzygium* germinate after fermentation of the fruits. Tidbury (1949) also advocated fermentation of fruits. When fruits of *Syzygium aromaticum* (Clove Tree) were

left to ferment for about three days the seeds were easily hulled, and such hulled seed produced "somewhat better seedlings" than unhulled. Germination was rapid, occurring within 12–14 days of sowing, and germination percentages were high, almost always above 90%. Hyland (1983) included seedling germination periods in his descriptions of some 50 Australian species of *Syzygium*. Germination periods ranged from 10 days to almost 10 months (300 days) and there was considerable within-species variation in germination time. In the same paper, species of *Acmena* were cited as having even longer germination times, ranging from 24 days to well over 2 years (860 days), while values for *Waterhousea* tended to be lower at 10–60 days. *Eugenia reinwardtiana* (Bl.) DC. and *Acmenosperma claviflorum* (Roxb.) E. Kausel were reported as having germination periods of 30–50 and 40–90 days respectively.

Ferreira (1982) studied germination of seeds of *Psidium acutangulum*, which had been treated with a 1% solution of a proprietary systemic fungicide after being removed from the fruit pulp. He found that germination occurred 30–100 days after sowing and that ca. 90% of seeds planted in loam (the most successful medium) germinated eventually. Lorenzi (1992) reported a similar range of germination times among 16 native Brazilian species (in eight genera) of Myrtaceae studied by him. The most rapid germination (10 days after sowing) was observed in *Eugenia pyriformis* Cambess., while some seeds of *Plinia edulis* (as *Marlierea edulis*) took up to 100 days to germinate. Gurgel and Soubihe Sobrinho (1951) reported germination times between 18 days (for *Psidium guajava*) and 73 days (for *Campomanesia* sp. as *Myrtus mucronata*). Levels of germination varied considerably (40–80%).

Lorenzi (1992) also reported seed viability periods. These were generally short (as little as 2 weeks in *Eugenia involucrata* DC.), but species of *Psidium* and *Acca* had longer seed viabilities of several months. Viability of seeds of *Psidium guajava* may exceed one year. *Blepharocalyx salicifolius* seeds lost viability within two months (Matos, 1994).

CONCLUSIONS

As might be predicted from their morphology, the Myrtoideae emerge from this review as a rather uniform group with respect to their overall pollination and dispersal syndromes. Most species diverge little from the apparently highly successful combination of small, short-lived flowers offering pollen to attract bees as pollinators and fleshy fruits adapted to endozoochory. However, it is possible to ob-

serve that more morphological diversification has arisen in characters linked to seed dispersal and seedling establishment than in those linked to pollination biology. For such a large group, the species exhibit an impressive uniformity with respect to general flower structure and pollen morphology.

The rather narrow pollination spectrum is reminiscent of other large groups with faithful bee pollination, e.g., Malpighiaceae (Anderson, 1979), Melastomataceae (Renner, 1989), and Solanaceae (Symon, 1979). Renner (1989) has suggested that such a lack of diversification may be the result of being "stuck on an adaptive peak." However, the data available suggest that the Myrtoideae run the gamut of flower-visiting bee taxa and fully exploit differences in bee behavior, such as buzzing abilities and trap-lining, the more highly evolved Apidae bee family being dominant. This is reflected in the considerable diversity in flower size, flowering phenology, and especially flowering strategies encountered. The breeding systems of the Myrtoideae vary from dioecy and complete self-sterility (with late-acting variants) through to self-compatibility and apomixis, suggesting that the Myrtoideae have successfully capitalized upon their bee pollinators, and diversified their reproductive strategies accordingly, to establish themselves as important elements in many different life-zones and habitats. In this respect, the Myrtoideae are similar to the Leptospermoideae, although this latter group has coevolved primarily with the most primitive flower-visiting bee family, the Colletidae, while simultaneously developing a secondary evolutionary line of bird pollination, which is very rare in the Myrtoideae. Certain specialized features of the floral biology of the Leptospermoideae are absent in the Myrtoideae, e.g., secondary pollen presentation, wet stigmas, and the presence of ovulodes in the ovary. Conversely, buzz pollination is, as far as we know, limited to the Myrtoideae. Within the Myrtoideae s.l. nectar-rewarding bird pollination systems, post-anthesis stylar extension, unitegmic ovules, and apomixis have only been registered in *Syzygium* (of the *Acmena* alliance) and may be restricted to this group (although the possibility of polyembryonic *Plinia* of the Myrtoideae s. str. also being apomictic cannot be discarded as yet).

The endozoochorous fruits of the Myrtoideae seem to be adapted to many different classes of dispersers, and this characteristic is probably the most important ecological difference as compared to the largely wind-dispersed Leptospermoideae. The Myrtoideae show a great variety in size, color, texture, and seediness of fruits, with the seeds also varying significantly in size, seed coat structure,

and embryo morphology. Pseudo-testa formation from the endocarp, testa formation from the outer integument only, oil glands in the embryo, and polyembryony are apparently restricted to the Myrtoideae.

Our knowledge of the reproductive biology of the Myrtoideae is still far from complete, and the following questions merit further investigation: Are inflorescence structure and flowering strategy correlated with habitat? Is flowering cued by abrupt fluctuations in humidity? How common is buzz pollination, and what are the adaptations and bees involved? Which birds are involved with bird pollination systems where petals are offered as a reward, why has this mechanism evolved, and how does it differ from nectar-rewarding bird pollination systems? How common is cryptic dioecy and what are the selective pressures maintaining this apparently expensive breeding system? What are the main agents of fruit dispersal and, in particular, how important is the role played by bats and other small mammals? Has co-evolution with parasites affected fruit and seed morphology? What is the nature of the mechanism which maintains preferential outcrossing and does more than one type of self-incompatibility exist in the family? Is there any relationship between apomixis, polyembryony, and chromosome number? The answers to such questions as these may have important and diverse implications. First, they may help to resolve some of the complex taxonomic problems in the Myrtoideae by helping to elucidate the functional significance of characters of taxonomic importance. Second, studies of breeding systems in particular should aid systematists, population geneticists, and ecologists in the interpretation of patterns of variation within and between populations and species. Third, this information may facilitate the genetic improvement of the several economically important species. Finally, a deeper understanding of the reproductive biology of a group that is of great ecological importance in several endangered tropical ecosystems may represent an invaluable contribution toward their conservation.

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